

Root disease can rival fire and harvest in reducing forest carbon storage

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Abstract. Root diseases are known to suppress forest regeneration and reduce growth rates, and they may become more common as susceptible tree species become maladapted in parts of their historic ranges due to climate change. However, current ecosystem models do not track the effects of root disease on net productivity, and there has been little research on how the dynamics of root disease affect carbon (C) storage and productivity across infected landscapes. We compared the effects of root disease against the effects of other types of forest disturbance across six national forest landscapes, 1990–2011. This was enabled by a monitoring tool called the Forest Carbon Management Framework (ForCaMF), which makes use of ground inventory data, an empirical growth model, and time series of Landsat satellite imagery. Despite several large fires that burned across these landscapes during the study period, retrospective ForCaMF analysis showed that fire and root disease had approximately equal impacts on C storage. Relative to C accumulation that would have occurred in their absence, fires from 1990 to 2011 were estimated to reduce regionwide C storage by $215.3 \pm 19.1 \text{ g/m}^2 \text{ C}$, while disease in the same period was estimated to reduce storage by $211.4 \pm 59.9 \text{ g/m}^2 \text{ C}$. Harvest ($75.5 \pm 13.5 \text{ g/m}^2 \text{ C}$) and bark beetle activity ($14.8 \pm 12.5 \text{ g/m}^2 \text{ C}$) were less important. While long-term disturbance processes such as root disease have generally been ignored by tools informing management of forest C storage, the recent history of several national forests suggests that such disturbances can be just as important to the C cycle as more conspicuous events like wildfires.

Key words: carbon; forest disturbance; forest management; forest pathology; root disease.

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INTRODUCTION

In forest ecosystems, managers are often interested in the impact of different management and disturbance processes upon fixation and storage of atmospheric carbon (C), an ecosystem benefit that may mitigate climatic effects of rising fossil fuel emissions. Biogeochemical models are a primary source of this information, and leading models allow assessment of the C storage impact of different disturbance processes such as fire

(Yang et al. 2015), timber harvest (Peckham et al. 2013), and insect outbreaks (Kurz et al. 2008a, Albani et al. 2010). Development of such models is often informed, and sometimes motivated, by empirical study of current or historical trends. However, despite long-standing evidence that forest root disease can profoundly affect forest development (James et al. 1984), ecosystem models generally ignore the effects of root disease. By excluding the long-term growth reductions that these pathogens can cause, models may

systematically overestimate C uptake over large regions (Dietze and Matthes 2014).

Root diseases have been observed to significantly increase tree mortality and reduce timber volume in coniferous forests of western North America (James et al. 1984, Hansen and Goheen 2000, Cruickshank et al. 2011), causing commercial timber losses and acting as a critical driver of forest succession patterns (Byler et al. 1990). In this study, we used a recently developed monitoring tool called the Forest Carbon Management Framework (ForCaMF) to compare the 1990–2011 C storage effects of root disease with those of other important types of disturbance (harvest, fire, mortality due to bark beetles) in six national forests where both fire and disease are known to be prevalent. A large impact of root disease in relation to other types of disturbance would suggest the need to address root pathogens in tools designed to support management of ecosystem services related to C storage, particularly in the large areas of western North America where root diseases are common.

Managers of the national forests studied here, all of which are in the U.S. Rocky Mountains (Fig. 1), have expressed concern that root disease greatly affects forest C stocks and that the effect may be larger than that of fire, timber harvest, or bark beetle outbreaks (USDA 2014a; James Morrison, USDA Forest Service, *personal communication*, 2012). Projections for the region show root disease to be a dominant disturbance agent affecting succession over the next few decades (Byler and Hagle 2000). The National Forest System (NFS) manages approximately 20% of the forestland in the United States, and each planning unit (national forest) is required to develop a baseline assessment of the influence of disturbance and management activities on C stocks (USDA 2011). Given evidence of the ecological importance of root disease in this region, assessment of root disease's impact on C therefore addresses a clearly articulated management need.

In contrast to the cyclical impacts of episodic disturbance events (e.g., harvests, fires), root diseases can persist on a site for decades, continuously reducing tree growth and net primary productivity, suppressing regeneration, and increasing mortality (Byler and Hagle 2000). Root diseases are caused by a variety of native

pathogen species that infect, decay, and kill tree roots, thus reducing the capacity of host trees to acquire water and nutrients. Infections can lead to tree mortality, but even without mortality, they cause a persistent reduction in tree growth and site productivity relative to uninfected sites (Cruickshank et al. 2011). Pathogens spread when infected roots come in contact with uninfected roots, often causing disease centers in which tree mortality creates visual gaps in the forest canopy (Hansen and Goheen 2000). In sites with severe root disease, newly regenerating trees in disease centers can be infected by dead trees or stumps remaining on the site, causing a persistent suppression of site productivity. In severe cases, root disease can stall forest succession in the seedling/sapling structure class and allow shrub invasion, at which time restoration may be difficult because root pathogens persist in dead roots and stumps, reinfesting natural or planted regeneration (Byler and Hagle 2000). In recent decades, several factors have contributed to an increase in root disease severity and extent in the northern and central Rocky Mountains, United States. Selective harvesting of *Pinus* species and fire exclusion have facilitated the spread of root disease by shifting species composition toward a greater proportion of Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and subalpine fir (*Abies lasiocarpa*), which are susceptible to infection (Byler et al. 1990, Hansen and Goheen 2000). Loss of western white pine (*Pinus strobus*), which is less susceptible to infection, to white pine blister rust (*Cronartium ribicola*), also contributed to a shift toward susceptible species (Byler and Hagle 2000). Lastly, commercial harvesting and thinning facilitated root disease spread because infected stumps and roots left after harvests retain pathogens that can rapidly spread to residual trees or regeneration (Hagle and Goheen 1988).

Similar risk factors exist across many ecosystems, and different pathogens affect ecological function across broad areas (Hicke et al. 2012). The objectives of this study were (1) to quantify the impact of root disease on C storage ($\text{g/m}^2 \text{ C}$) across large areas by contrasting storage under monitored and root disease-free scenarios and (2) to compare this impact with the effects of more immediately visible disturbance agents such as

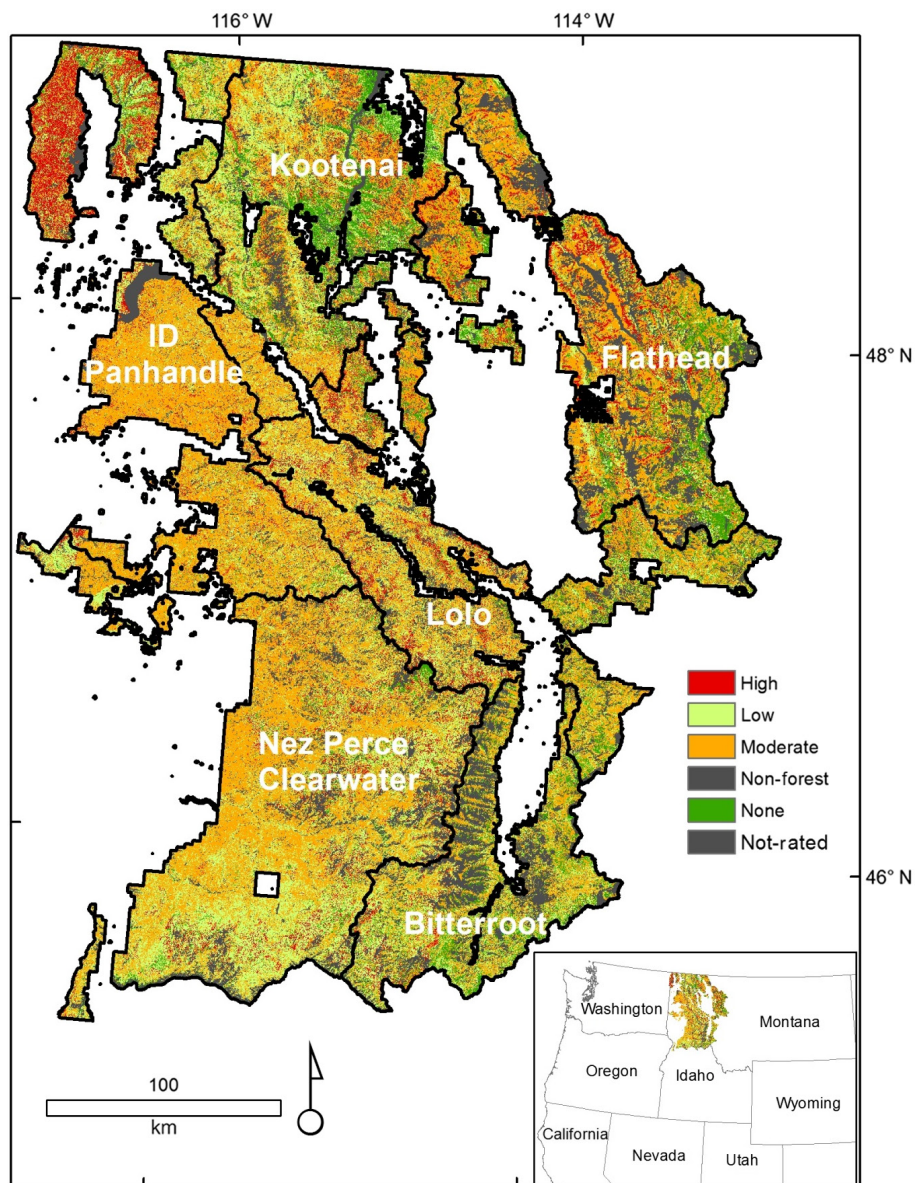


Fig. 1. Six national forests in the northern Rocky Mountain region, United States, and the extent of root disease hazard ratings developed by the Forest Service (USDA 2014b).

fire, which is common and intensively managed in the region.

METHODS

The reader is directed to supplemental detail contained in three supplemental appendices: Error Simulation through PDF Weaving (Appendix S1), Maps and Reference Data Informing ForCaMF

Analysis (Appendix S2), and Implementation of Root Disease in ForCaMF (Appendix S3).

Study area

The study domain included six national forests in the northern Rocky Mountains, United States, namely the Lolo, Bitterroot, Nez Perce-Clearwater, Idaho Panhandle, Kootenai, and Flathead National Forests. The forests lie west of

the Continental Divide and cover an area of over 6 million hectares (Fig. 1). The majority of the region's forests are coniferous, dominated by Douglas fir, grand fir, and subalpine fir. Fire is known to be frequent and is growing in importance across these ecosystems (Higuera et al. 2015). Many aspects of fire effects and fire management in the region have been studied, including in the areas of air quality (e.g., Urbanski 2013), wildlife (e.g., Hutto 1995), and hydrology (e.g., Goode et al. 2012). Agency records show declining harvest levels through the period of the 1990s throughout the region. The six national forests studied are located in northern Idaho and western Montana, where root diseases are important agents of ecosystem change (Hagle et al. 2000). The apparent extent and severity of root disease has raised concern among forest managers regarding its effects on C storage potential.

Overview of the ForCaMF

ForCaMF is a modeling and monitoring tool that, like the Carbon Budget Model of the Canadian Forest Sector (Kurz et al. 2009), uses empirical yield curves to understand C dynamics associated with management and disturbance. As such, ForCaMF's growth and decay functions are based upon observed long-term averages and are not sensitive to climatic or atmospheric variables that may change over time. For this reason, ForCaMF has only been applied retrospectively to the recent decades from which most growth and yield data have been collected.

ForCaMF may be used to assess the relative impact of different types of disturbance, including root disease, on short-term landscape-level carbon storage. Impact of disturbance factor F (e.g., harvest, fire, bark beetle attack, root disease) is estimated as the difference, D_F , in the landscape's non-soil C stocks between a scenario where no disturbances occur during the observation period and a scenario where only disturbance factor F occurs (Fig. 2). Each scenario includes normal density-dependent tree mortality that is not attributable to disturbance. As will be detailed below, estimates of C storage under each scenario are derived by overlaying mapped conditions of starting vegetation with maps of subsequent disturbances, and by then interpreting consequent changes in C stocks using

regionally generalized, disturbance-specific C accumulation functions.

An estimate of D_F is produced for every year (1990 to 2011 in the current study) as the difference between all non-soil stocks (1) when all preceding type- F disturbances (since 1990) are taken into account and (2) a no-disturbance scenario (N), summed over all spatial simulation units, i (Eq. 1).

$$D_F = \sum_{i=0}^n (C_{i(N)} - C_{i(F)}) \quad (1)$$

Simulation units (i) are composed of groups of 30-m map pixels sharing exactly the same mapped starting conditions and disturbance histories, aggregated to reduce the computational burden of subsequent probabilistic operations. In this study, 10-ha simulation units were used, reducing computational requirements by two orders of magnitude. Maps and reference data are detailed in Appendix S2; this section presumes the availability of starting condition (circa 1990) maps of forest type and live tree C, along with maps of the type, magnitude, and timing of disturbance from 1990 to 2011. Carbon storage (Mg C across all non-soil pools) in a particular simulation unit (C_i) under any scenario is a function of the amount of area it represents, its disturbance history, and mapped starting (1990) conditions that link it to a mean C accumulation function (Fig. 2; Appendix S2: Eq. S1). Raymond et al. (2015) described how a representative sample of inventory plots from the U.S. Forest Service Forest Inventory and Analysis (FIA) Program can be used with the carbon submodel available in an empirically calibrated simulation tool called the Forest Vegetation Simulator, "FVS" (Reinhardt and Crookston 2003), to develop regionally representative C trajectories for a range of disturbance scenarios or in the absence of disturbance (Fig. 2). FVS is currently used to support a range of management planning decisions across the National Forest System (e.g., Henderson 2008).

The lower right corner of Fig. 2 illustrates the process of generating regionally average C accumulation functions. FVS typically operates at the stand level, informed by inventory plot or stand examination data, allowing C accumulation patterns to be projected following specified management or disturbance events (or in the absence of

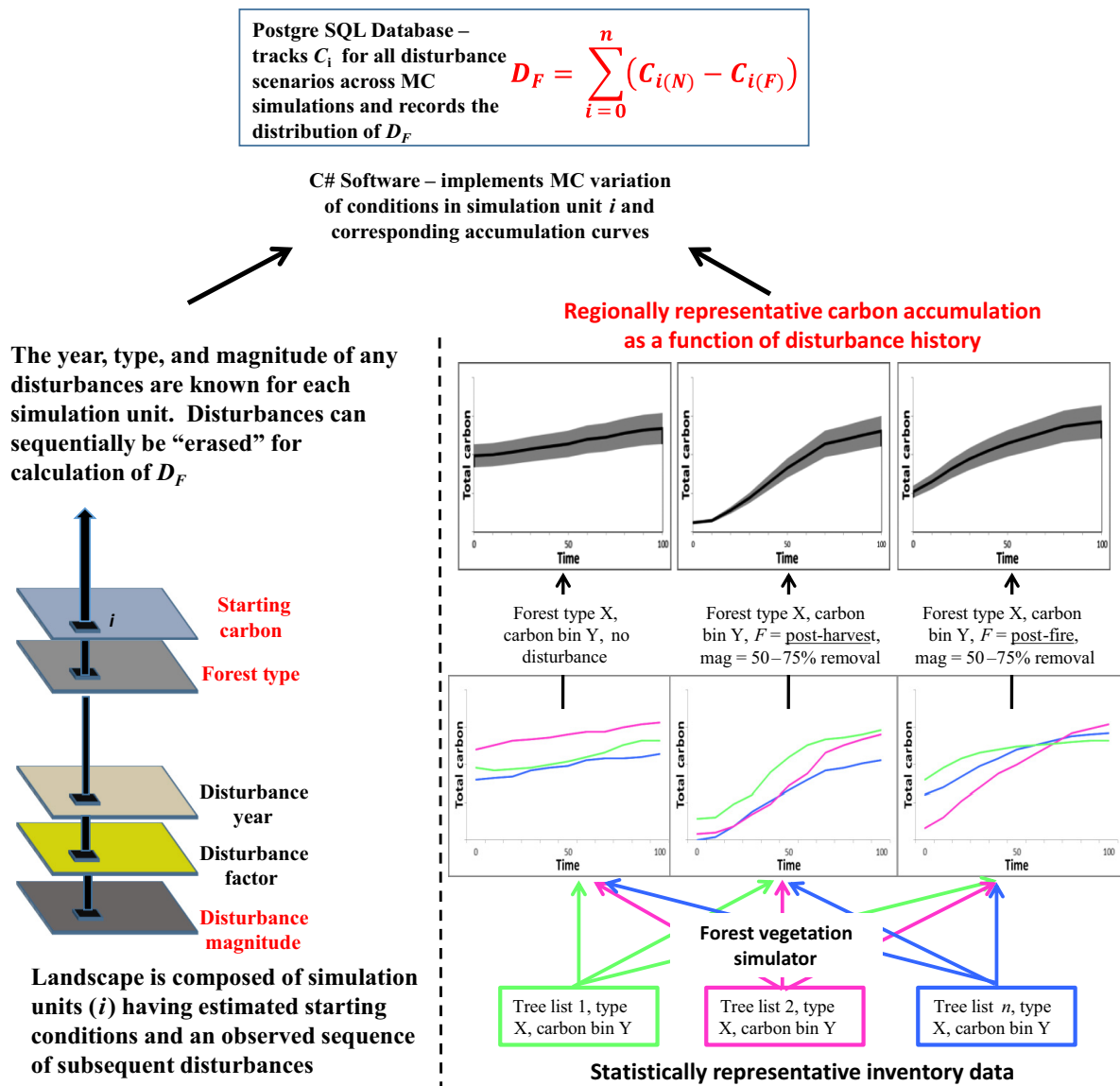


Fig. 2. Flowchart of ForCaMF data sources, processes, intermediate products, and output. Components in red are treated as random variables in Monte Carlo error simulations.

disturbance). Carbon stocks in all non-soil pools are tracked independently following disturbance, with transfers among pools controlled by the carbon submodel in response to patterns of mortality, combustion, and/or removal generated by the base model (Reinhardt and Crookston 2003). Carbon in trees killed by insects, for example, is transferred to standing and then down dead pools before eventual release to the atmosphere. Transfer rates are based upon regionally

specific parameters that are determined by the Forest Service National Forest Management Service Center using the best available empirical calibration information.

ForCaMF adapts this stand-level tool to generate regional C dynamics by submitting all available FIA plots (5342 plots were used in this study) to FVS simulation over a range of disturbance types and magnitudes, with outputs describing C loss and recovery either in the absence of

or following disturbance/management. These outputs are summed across C pools for use in ForCaMF, but reflect the disturbance-sensitive transfers described above. FVS parameters, controlled by “keywords” (which in this study were largely supplied by regional NFS managers), are iteratively varied for each plot to produce hundreds of thousands of C accumulation projections for the region.

These projections are then grouped by starting conditions and the nature of the simulated disturbance, with the constraint that a group may contain no more than one randomly selected simulation from each plot. A non-parametric spline-based regression process then determines the average annual C density for each group over a 100-year period, producing at the same time confidence intervals for that mean C trajectory for every year (Raymond et al. 2015, gray regions in Fig. 2). Although the resulting C accumulation functions cover 100 yr, ForCaMF has thus far been limited to retrospective studies such as this one, using only approximately the accumulation function’s first 30 yr, because of uncertainties related to longer-term impacts of changing atmospheric and climatic conditions on growth rates.

ForCaMF uses the resulting empirical mean C accumulation or recovery functions to control the amount of C that is assigned to each simulation unit, i , over time in response to i ’s mapped starting conditions and disturbance record (see Appendix S2 for supporting inventory and map data). Each simulation unit starts (in 1990 in this investigation) with the regional mean amount of C for that unit’s starting conditions (defined by forest type and level of live tree C, as described below) and accrues C according to the appropriate “undisturbed” C accumulation function until a disturbance occurs. When a disturbance occurs, i is switched to the appropriate post-disturbance C recovery function, which is used to determine C storage as a function of time since disturbance (Healey et al. 2014).

It is possible to associate individual simulation units with particular FVS C accumulation and recovery functions because both the maps used to create the simulation units and the rules governing the grouping of FVS simulations employ the same classification rubric. In this investigation, all simulations and simulation units were grouped on the basis of forest type group (there

were six occurring in the FIA sample) and the level of starting live tree C (FIA variable “CARBON_AG”; Woudenberg et al. 2010). Thresholds used to define the live tree C bins were chosen to distribute FIA plots and their subsequent simulations into four approximately equal groups. For scenarios involving disturbance, simulations and map units were also grouped by the type and magnitude of disturbance. Four types of disturbance were included in this study, three of which (fire, bark beetle attack, and harvest) were divided in both simulations and maps into four levels of magnitude (0–25, 25–50, 50–75, and 75–100% canopy cover loss). Magnitude for the other type of disturbance (root disease) was divided into three levels (0–33, 33–66, and 66–100% canopy loss). This totaled 384 types of growth or recovery functions attributable to the mapped conditions used to define each simulation unit: undisturbed growth in 24 type-by-carbon starting conditions, four levels of magnitude for three types of disturbance, and three levels of magnitude for one type of disturbance, each with 24 possible (forest type $\times$ C level) starting conditions.

Association of simulation units with the correct accumulation or recovery curves over time, along with tallying assigned C densities across the landscape by year (Eq. 1), was mediated by ForCaMF’s C#-based software (Fig. 2). Determination of D_F , the relative impact of type- F disturbance, requires all non- F disturbances be “erased,” with affected simulation units instead assigned to undisturbed growth curves (Eq. 1). This was sequentially carried out by ForCaMF’s software for each F . Thus, the impact of a particular type of disturbance, that is, immediate C emissions plus any subsequent depression of net ecosystem productivity through respiration of newly dead material, was measured against what would happen in the absence of that disturbance process.

Because ForCaMF’s primary output (D_F) involves a comparison of C storage under observed disturbance patterns against a hypothetical “no-disturbance” scenario, direct validation was not possible. However, errors in the calculation of D_F are simulated and integrated through a Monte Carlo process directly constrained in several dimensions by external monitoring data. As described in Appendix S1, D_F was calculated 500 times using values for forest

type and level of starting C that were probabilistically varied, implementing a correction factor that forced simulations to match the confidence envelope of FIA's estimate. Specifically, values were varied in a way that reflected both the pixel-level accuracy of the starting C and forest type maps (assessed at the location of available plots) and any difference between map totals and FIA population estimates at the scale of the national forest. The process of assimilating map and reference values in constraint of error simulations is called "PDF Weaving" and is described in Appendix S1 and by Healey et al. (2014). As error simulations potentially changed the attributes of each simulation unit, the Monte Carlo process also varied associated C accumulation functions, using a process also described in Appendix S1.

Fig. 2 displays all factors treated probabilistically in red. The predicted C stocks in each simulation unit under each disturbance scenario, F , were stored in a PostgreSQL database. Landscape-level differences in C storage attributed to each disturbance factor (D_F) were calculated annually in each simulation, and the variation in D_F across simulations was taken as an empirical estimate of integrated uncertainty. Specifically, 2.5th and 97.5th percentile values of D_F were identified as an empirical 95% confidence interval. The aforementioned Monte Carlo process addressed errors at the level of the national forest, not the region. Regional averages were derived by a probabilistic weighted averaging process that varied with forest-level results according to their own uncertainties. The spread of resulting weighted averages was used to determine empirical 5% confidence intervals. This operation assumed that the errors in one forest were independent of errors in other forests, which was reasonable for all variables except "forest type," which was derived for each national forest by subsetting the same national-scale map. As a result, regional-level confidence intervals were likely slight underestimates.

RESULTS

Map results and validation

Fig. 3 shows temporal patterns of harvest, fire, and bark beetle disturbance over each of the national forests studied, as represented in the maps described in Appendix S2. Of those three

disturbance factors, fire was dominant in most of the national forests over the period 1990–2011. Although there were often years when no fire occurred within forest boundaries, large areas could be affected; in the year 2000 alone, more than 10% of the Bitterroot National Forest burned. In forests where harvesting was significant, the percentage of the affected area declined through the 1990s. Canopy loss to bark beetle activity was less common than the other two processes, but did sporadically occur across the region.

As described in Appendices S2 and S3, root disease occurrence could not be mapped. An alternative strategy was used as a first approximation based on the best available data. A risk map (Fig. 1) was used to target Monte Carlo simulation of disease at rates that matched the disease prevalence observed in the FIA sample. The root disease hazard map showed infection risk across three hazard levels for 63% of the landscape, while the FIA sample suggested infection of 29% of the landscape across three levels of severity (Table 1). Mapped severity levels (including a class for no root disease) matched field observations at 46% of the plots. This success/failure rate and the validation results presented in Table 1 were used to constrain probabilistic ForCaMF simulations through the "PDF Weaving" process described in Appendix S1 and by Healey et al. (2014). Monte Carlo simulations were constrained to reflect the prevalence of root disease in the FIA sample; the root disease risk map was only used to target simulation units for FIA-based rates of infection. Pixel-level accuracies for the six-class forest type map, four-class starting live tree C map, and four-class disturbance magnitude map were 56%, 53%, and 32%, respectively.

Carbon dynamics at the forest stand scale

Regional C accumulation curves derived from FIA and FVS for fire, harvest, and bark beetle activity were described in detail by Raymond et al. (2015). Stand-level simulations of root disease with FVS show that over time, root disease greatly reduces total C stocks relative to stands without root disease. Reductions increased with increasing severity and were higher in stands dominated by tree species with high susceptibility to root disease (Table 2).

Accumulation of total non-soil C over time in stands with root disease exhibits a distinctly

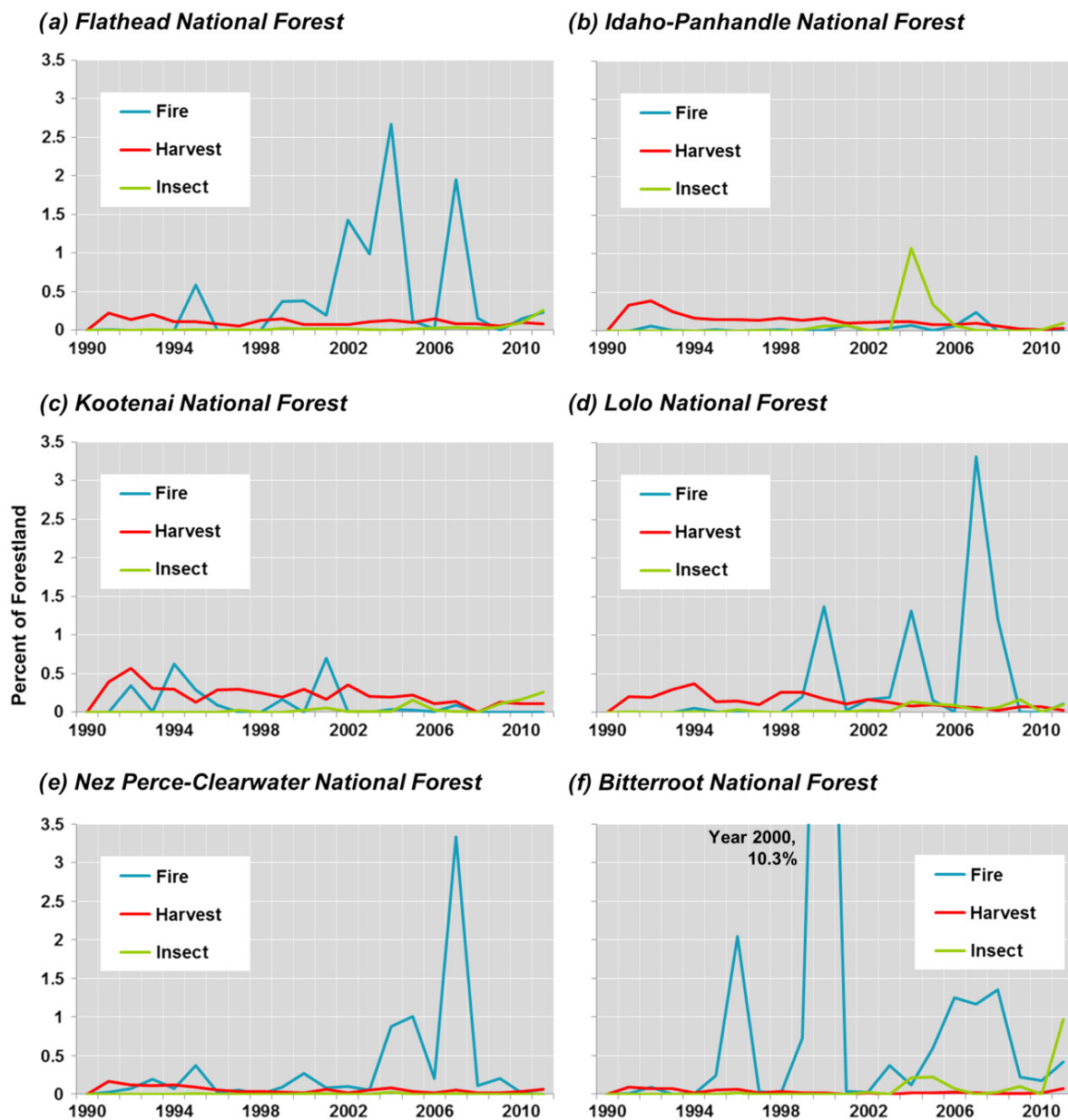


Fig. 3. Disturbance rates for each national forest by year and disturbance type. Rates were derived from maps produced by stand-level manual integration of Landsat and high-resolution imagery along with agency fire, harvest, and insect records (Appendix S2).

different pattern than accumulation of C in stands following an episodic disturbance (bark beetle outbreak, fire, or timber harvest), wherein initial net emissions are followed by a period of accumulation. Fig. 4 shows examples of C accumulation functions used to simulate changes in forest C over time in ForCaMF for one forest type (shade-tolerant species mix), one relatively high

level of initial live tree C, and all levels of severity for each of the four disturbance types. Stands with episodic disturbances (fire, bark beetle outbreaks, and harvest) of high severity exhibited a period of post-disturbance decline in C during which decomposition of biomass killed by the disturbance exceeds C uptake from regeneration and regrowth. Stand C accumulates again when

Table 1. Comparison of FIA subplot observations of root disease severity class with spatially correspondent map classes in the 30-m resolution root disease hazard map (USDA 2014).

Map severity	FIA severity				Percentage of total	Map calls correct, %
	None	Low	Medium	High		
None	5453	450	193	18	37	89
Low	2652	1039	343	22	25	26
Medium	2871	1159	886	70	31	18
High	657	293	161	51	7	4
Percentage of total	71	18	10	1		
Field calls correct, %	47	35	56	32		46

regrowth and regeneration exceed decomposition, and the time at which this occurs is a function of disturbance type and severity. In contrast, stands infected with root disease showed a gradual decline in stand C, the magnitude of which was a function of severity. This decline persisted for the 100-year simulation for moderate- and high-severity root disease, although the rate of C decline slowed. Stand C increased initially in

stands with low-severity root disease, although at a slower rate than in stands without root disease, but began to decline at the end of the 100-year simulation (Fig. 4).

Carbon dynamics at the national forest scale

For the 21-year period of the national forest-scale simulations, root disease greatly reduced total forest C (Mg/m² C) relative to no disturbance

Table 2. Mean change over 100 yr in non-soil carbon (Mg/ha) in stands affected by the three levels of severity used in this study's FVS simulations.

Total C (Mg/ha) gain or loss (percentage of undisturbed C) at 100 yr					
Dominance type	Carbon level	None	Low	Moderate	High
<i>Abies lasiocarpa</i>	1	96	66 (-31)	17 (-82)	13 (-86)
	2	84	42 (-51)	-19 (-123)	-32 (-138)
	3	58	23 (-60)	-37 (-164)	-59 (-202)
	4	43	14 (-67)	-53 (-223)	-82 (-293)
<i>Pseudotsuga menziesii</i>	1	134	62 (-54)	29 (-79)	22 (-84)
	2	88	27 (-70)	-14 (-116)	-29 (-133)
	3	71	11 (-83)	-39 (-155)	-61 (-186)
	4	57	2 (-96)	-65 (-214)	-98 (-272)
Shade-tolerant mix	1	146	85 (-42)	34 (-77)	18 (-88)
	2	110	55 (-50)	-10 (-110)	-40 (-137)
	3	91	45 (-51)	-27 (-131)	-65 (-171)
	4	64	22 (-66)	-57 (-189)	-104 (-261)
Shade-intolerant mix	1	115	97 (-16)	71 (-38)	56 (-51)
	2	68	59 (-13)	27 (-60)	12 (-84)
	3	70	50 (-29)	13 (-81)	-6 (-109)
	4	41	24 (-41)	-23 (-156)	-50 (-222)
<i>Pinus contorta</i>	1	91	78 (-14)	37 (-59)	17 (-81)
	2	55	43 (-22)	-3 (-105)	-23 (-142)
	3	43	31 (-28)	-17 (-140)	-41 (-195)
	4	30	19 (-37)	-34 (-210)	-64 (-313)
<i>Pinus ponderosii</i>	1	109	105 (-4)	89 (-18)	72 (-34)
	2	85	77 (-8)	52 (-39)	32 (-62)
	3	65	60 (-8)	34 (-48)	15 (-77)
	4	63	48 (-22)	8 (-87)	-21 (-132)

Notes: "Carbon level" reflects the four classes of the FIA variable CARBON_AG used here. Negative values indicate a carbon source for the 100-year simulation. Negative values for the percentage difference from total carbon of the undisturbed stands are the loss of C storage potential caused by root disease relative to stands without root disease.

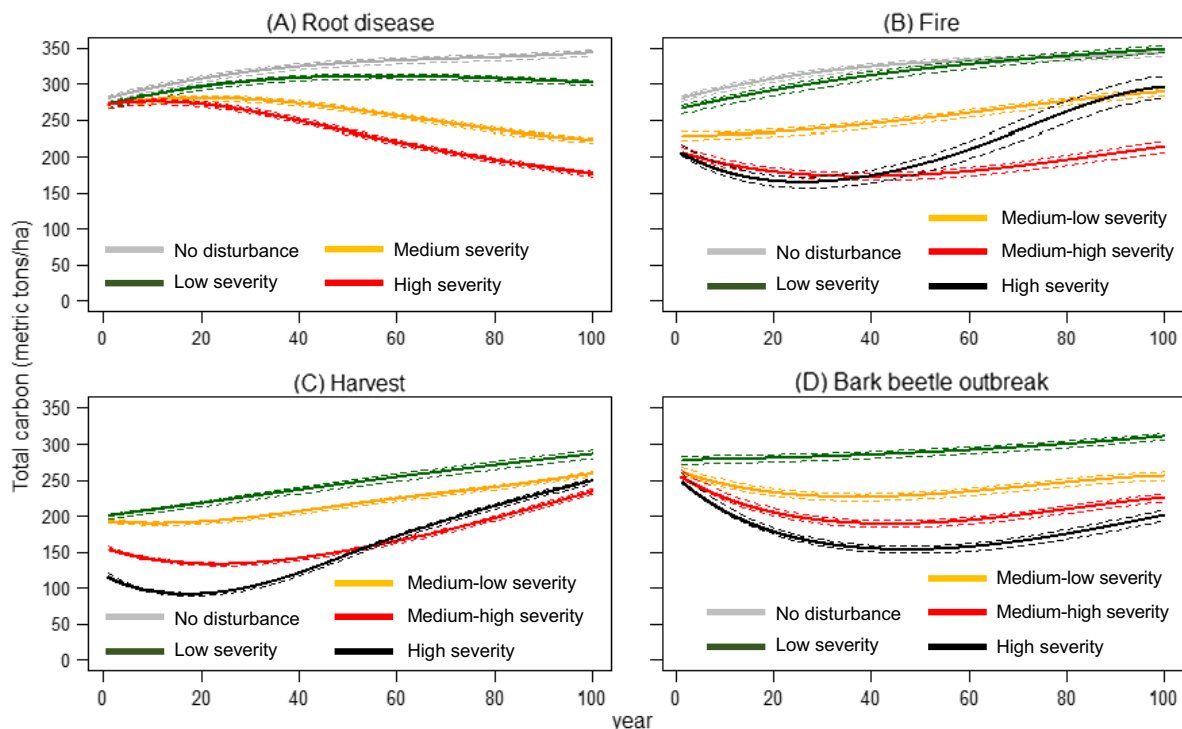


Fig. 4. Total non-soil stand carbon as a function of time since disturbance for four disturbance types: (A) root disease, (B) fire, (C) harvest, (D) bark beetle outbreak. C dynamics are shown for one of six forest types (shade-tolerant species mix; TMIX) and one of four levels of initial live tree aboveground C ("high"). Solid lines indicate the mean response of multiple stands for varying levels of disturbance severity. Gray is no disturbance, and green, yellow, red, and black are low- to high-severity disturbances, respectively. Dashed lines show the standard error of the model prediction.

for all six national forests (Fig. 5). Fig. 5 shows D_F across the study period for each disturbance type in each national forest. Error bars represent 95% confidence intervals observed across 500 simulations. Confidence intervals for F = root disease were larger than for other disturbance factors because, unlike fire, harvest, and bark beetles, root disease could not be reliably mapped, and its area was therefore subject to probabilistic variation (as described in Appendix S3).

In the Idaho Panhandle and Kootenai National Forests, root disease reduced forest C stocks more than any other disturbance, and this dominant effect persisted for the 21-year period. Harvest was the second largest cause of reduction in C storage relative to undisturbed scenarios, whereas fire and bark beetle outbreaks had a relatively small effect on total C stocks. On the Kootenai National Forest, all disturbances reduced C storage by $381.9 (\pm 121.5) \text{ g/m}^2 \text{ C}$ and

root disease alone reduced C storage by $180.5 (\pm 119.5) \text{ g/m}^2 \text{ C}$, 47% of all C storage reductions via disturbance (Fig. 5). On the Idaho Panhandle National Forest, disturbance reduced C storage by $443.7 (\pm 171.1) \text{ g/m}^2 \text{ C}$, of which root disease accounted for $269.9 (\pm 161.9) \text{ g/m}^2 \text{ C}$, or 60% (Fig. 5).

On the Nez Perce-Clearwater, Flathead, and Lolo National Forests, root disease and fire caused a similar reduction in C storage potential relative to the undisturbed scenario over the 22-year period. On the Nez Perce, Flathead, and Lolo National Forests, total loss of potential C storage at the end of the period via disturbance was $533.1 (\pm 160.5)$, $520.4 (\pm 128.9)$, and $449.7 (\pm 110.9) \text{ g/m}^2 \text{ C}$, respectively (Fig. 5). On the Nez Perce-Clearwater National Forest, 46% of C storage losses were attributed to fire and 47% were attributed to root disease. On the Flathead National Forest, 54% of losses were attributed to

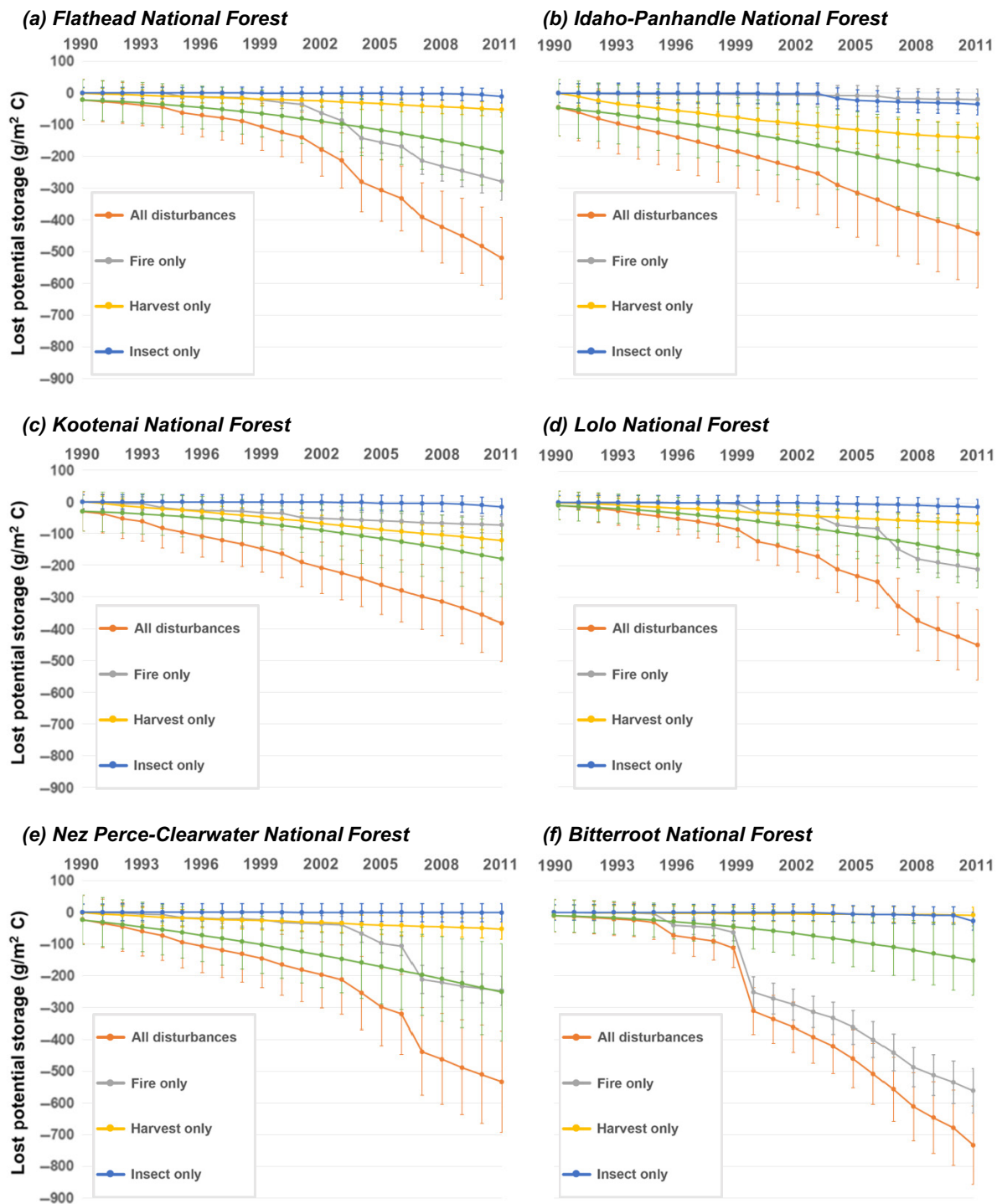


Fig. 5. National forest-scale impact of four types of disturbance upon non-soil C storage from 1999 to 2011. Values at each point in time represent D_F (Eq. 1 and Fig. 2), the difference between the total C storage under a no-disturbance scenario and a scenario where only disturbances of type F have occurred since 1990. Error bars represent the observed 2.5th and 97.5th percentile values of 500 simulations.

fire and 36% were attributed to root disease. On the Lolo National Forest, 47% of the losses were attributed to fire and 37% were attributed to root disease. In individual years with extensive area burned, C losses due to fire caused a relatively sharp decline in forest C stocks and an increase in D_F . In contrast, the magnitude of the effect of root disease on total C stocks at the national forest scale was relatively stable, with root disease causing a persistent reduction C storage potential over the 22-year period. In these three national forests, bark beetle outbreaks and harvest caused a relatively small decline in total forest C stocks over the 21-year period.

On the Bitterroot National Forest, the relative effect of disturbances on forest C differed greatly from the other national forests in the region. Fire caused the largest reduction in C storage relative to other disturbances, primarily because of extensive fires that burned in 2000. Total C storage reduction relative to an undisturbed scenario was $733.1 (\pm 124.1) \text{ g/m}^2 \text{ C}$ over the 22-year period and fire caused 77% of this reduction (Fig. 5). Root disease was the second largest cause of reductions in C storage potential, but only at 21%. Harvest and bark beetle outbreaks had only a minor effect on total forest C storage potential. Regionwide, when forest-level impacts of disturbance on carbon storage (D_F) were weighted by the area of each forest, the impact of disease on 1990–2011 C storage ($211.4 \pm 59.9 \text{ g/m}^2 \text{ C}$) was nearly the same as the impact of fire ($215.3 \pm 19.1 \text{ g/m}^2 \text{ C}$). Harvest ($75.5 \pm 13.5 \text{ g/m}^2 \text{ C}$) and bark beetle activity ($14.8 \pm 12.5 \text{ g/m}^2 \text{ C}$) were significantly less important on these national forests during the study period.

DISCUSSION

Fig. 4 shows that at the stand level, the effect of root disease, particularly at low (green line) and medium (gold line) severities, does not immediately cause large C storage differences in relation to undisturbed stand development (gray line). Differences do increase after several decades because of continued reductions in growth and regeneration rates in infected stands, but only 21 yr of impact is assessed here. The per-hectare impact of disease for any 1 yr was therefore relatively low.

However, root disease affected much more area than other types of disturbance, and unlike episodic disturbances, disease exhibited no distinct C recovery phase in our regionally representative C accumulation curves (Fig. 4). According to our regional disturbance maps, 10.1% of forested areas were affected by fire, harvest, or bark beetles at least once between 1990 and 2011. Inventory data suggested that almost three times that area was infected with root disease (Table 1). The C loss associated with root disease is perhaps not as readily observable as losses associated with fires or harvests, but because disease can be so much more pervasive, and because of its continued impact on a site, it can be, as it was in these landscapes, a dominant factor in net C uptake and storage.

This finding is relevant to both managers and modelers. The C implications of other, more visible, types of disturbance are already addressed by some ecosystems models (e.g., Bond-Lamberty et al. 2007, Raffa et al. 2008, Meigs et al. 2011) and are broadly understood to impact ecosystem services related to storage of greenhouse gases (e.g., Kurz et al. 2008b). Integration of event-oriented processes like fires, insects, and harvest into ecosystem models has been made possible by successful monitoring through remote sensing (e.g., Healey et al. 2008, Huang et al. 2010, Meigs et al. 2015), but recent advances have indicated that the complete disturbance picture is much broader. Cohen et al. (2016) studied historical imagery acquired for a random sample of plots across the United States and found that disturbance related to “forest decline,” which includes disease, was by far the most common disturbance process in the western part of the country, affecting up to 6–7% of the landscape in a given year. The current study documents that these disturbances can have strongly negative consequences on C storage.

Understanding likely trends in root disease and other pathogens under a changing climate is complicated by variation in the responses of both hosts and pathogens. Some root pathogens occur more frequently in wetter forests, suggesting that these forest types could experience an increase in root disease infection if precipitation increases with climate change (Kliejunas 2011). On the other hand, root disease extent may also expand in forests that experience drier

conditions with climate change. In general, it is thought that the role of pathogens as disturbance agents will likely increase because their ability to adapt to new climatic conditions will be greater than that of their long-lived hosts (Sturrock et al. 2011).

To the degree that pathogens such as root disease are both a sign and an agent of ecosystem change in response to climate change, it is important that models designed to predict C flux address their activity. As this study documents, root disease can significantly reduce net C storage. Because infection can persist for decades before further disturbance or succession causes compositional shifts, models that do not account for disease may significantly overestimate net productivity.

An obstacle to including root disease in ecosystem process models is that net primary productivity is often treated as a function of stand age. This kind of function can be calibrated by comparing observations of age and biomass across a large number of inventory plots in a so-called chronosequence (e.g., Law et al. 2003, Williams et al. 2012). Under this system, if root disease does not kill trees, it will not adjust stand age and will therefore not affect productivity. Even if some trees are killed, it is unlikely that corresponding changes of the age variable will properly reflect the reduced growth of surviving trees and the suppression of regeneration associated with this kind of disturbance. The ForCaMF approach, using an empirical growth model and a representative sample of field plots to identify average C densities following disturbances of different types and magnitudes, avoids shortcomings of models based upon stand age. However, ForCaMF's empirical basis is not well suited for simulation of changing climatic or atmospheric conditions.

An expedient adaptation to account for the impact of root disease in process models may be to apply a productivity reduction factor in ecosystems with significant infection rates. Calculated net productivity reduction due to root disease in the national forest landscapes studied here ranged from 150 to 270 g/m² C (weighted mean of 210.5 g/m²), which could be translated into an annual average impact over the 21-year observation period. Inventory records, where available, could be used to guide application of such

reduction factors. Although the FIA root disease severity variable used here is a local enhancement of the national FIA suite of variables, mortality due to disease is measured throughout the country (Shaw et al. 2005) and could be used to determine disease extent.

More traditional process-oriented approaches may also be feasible. Dietze and Matthes (2014) proposed a framework for incorporating forest insects and pathogens (including root diseases) into ecosystem process models. Under this framework, root disease was grouped with insects and nematodes that attack tree roots, with primary effects modeled as increased root turnover. A limited implementation of this framework at a site in Oregon demonstrated significant impacts of root pathogens on carbon storage and other biological and physical parameters.

Abundant research supports management decisions related to C and fire (e.g., Ager et al. 2010, Amiro et al. 2010, Hurteau and North 2010), and this study shows that the effect of root disease on C can exceed the impact of fire even on landscapes where fire is extremely common. Root disease management strategies may include actions favoring species that are more climatically adapted or that are resistant to the pathogen, as well as activities that increase age range and structural diversity across the landscape (Morrison and Mallett 1996, Klopfenstein et al. 2009, Woods et al. 2010, Sturrock et al. 2011). Better models would provide insight into the need for and benefits of these activities with respect to C storage.

CONCLUSIONS

This research shows that, where prevalent, root disease can significantly reduce C storage, often more than other more visible disturbances. Analysis using FIA data, historical disturbance records, and a widely used forest dynamics model showed that the C consequences of root disease in this region are similar in magnitude to those of fire and are much greater than the impacts of bark beetle and harvest. Impacts in this study were defined not only in terms of direct emissions through combustion and decomposition of dead trees, but also in terms of reduced productivity via suppressed growth. While initial losses of C to root disease are

generally lower than losses to other types of disturbance at the stand scale, the prevalence and persistence of root disease following infection mean that root disease is reducing C storage potential on a comparatively large portion of the landscape in any 1 yr—approximately 30% in this study vs. less than 2% for other disturbances. This result signals a potential need in many regions to account for root disease and other pathogens in ecosystem models.

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